

MISCELLANEOUS NOTES ON AUSTRALIAN DIPTERA. X.

DISTRIBUTION, CLASSIFICATION AND THE *TABANUS POSTICUS*-GROUP.

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(One Text-figure.)

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THE DISTRIBUTION OF THE DIPTERA BRACHYCERA.

Historical.—When collecting evidence of the remarkable affinity between the Australian and South American Diptera Brachycera, an investigation starting in 1918, the intention was to link this with the hypothesis of "floating continents", as the idea existed that this might be helpful in establishing the main thesis propounded by Wegener. The subject was pursued through short talks with the late Professor L. Harrison of the University of Sydney, the late C. Hedley of the Australian Museum, and others with knowledge of animal distribution; but with the late E. W. Ferguson the theory was only discussed in its effect upon genus *Tabanus*, part of which showed possible antarctic origin. I attribute below, by names in parentheses, impressions that I had gained by criticism of the antarctic theory of origin received from this generation of former workers, who studied the general problem of animal distribution, but it was not until I had a talk with Mr. H. Longman of the Queensland Museum, that I finally abandoned the above theory in 1922 and turned attention to the view that the whole of the Brachycera may have been derived from a sequence of northern invasions.

To forestall criticism of statements below, it is necessary to point out that *Pelecorhynchus mirabilis* reverts to the *personatus*-group, the two others belong to the *fusciger*-group, as my *fulvus*-group, accepted by Mackerras and Fuller as a colour group, is evidently a complex. Also Hermann records *Apiocera* from North Borneo presumably on a misreading of a handwritten label marked "M'bourne", several of which I have seen on Victorian specimens of the same species as that identified by Hermann.

The Antarctic Theory of Origin.—Mackerras and Fuller (1942) have discussed how the genus *Pelecorhynchus* may have become isolated in the south-east area of continental Australia, the island of Tasmania and Chile. They explain this distribution upon the theory of "antarctic" origin, that is to say, the genera so distributed evolved in the southern hemisphere at the time when it was theoretically possible for them to have had a wide dispersal in the temperate climate of southern land connections, the Gondwana Land, since disrupted.

Quite apart from the difficulty of fixing the geographical location as a source or origin for any winged animal type (Hedley) is the major difficulty of accepting the antarctic hypothesis due to the time limits (Harrison). This difficulty lies in the idea that *Pelecorhynchus* and similarly distributed genera are all highly evolved along their respective lines and yet each must represent a faunal element existing anything up to one hundred million years back to its genesis, developing and maintaining so close an affinity in Australia and Chile as to have the Chilean forms placed in Australian groups after, say, forty million years' isolation. The epochs in time estimates are given by A. L. du Toit in *Our Wandering Continents* (1937, p. 48), and allowance has been made for the breaking up of the continental mass depicted there for Eocene times (p. 18). Expressed in these figures, the objection is more easily comprehended, and also it will be noted that only the more advanced of the two Australian groups comprising *Pelecorhynchus* is retained in Chile, whereas the more primitive one is almost exclusively represented in the Tasmanian fauna, a feature that fits best the opposed theory. Moreover, if Philip be justified in placing the genus *Bequaertomyia* in the *Pelecorhynchinae*, then much of the argument for the antarctic theory of origin must collapse.

The Theory of the Northern Invasion.—For the purpose of orientating the whole outlook, one can assume that every major group of the Brachycera, at least down as far as subfamilies and even tribes, had its origin in tropical and subtropical climates. This may be substantiated on the idea that only in such places does one find the optimum breeding rate and the greater competition for survival amid an abundant competitive fauna. The evolution rate would thus be enhanced compared with that under conditions in more temperate zones. In accord with this, there occurred also the gradual displacement of the original type in the tropical region by later evolved types, the primitive ones surviving best in the least accessible places to where they had penetrated. Moreover, this gives a radiation polewards in diminishing proportion of species and genera, with a trend towards preserving a higher proportion of primitive characters in regions most remote from the place of origin. Australia, being comparatively isolated, may afford a better refuge for survival of primitive characters than most continents (Longman).

If the idea be well founded, then one would expect to see parallel evidence of the same poleward dispersal with recent genera permeating all regions, dominant in the tropics and reduced in the outer ones where a trend towards retaining primitive structures on such recent genera would also be noted.

This condition is apparent in *Sarcophaga sensu stricto* (Hardy, 1943), a genus undoubtedly splitting into three recognizable subgeneric units between Australia and India. The subgenus *Chrysosarcophaga* seems to be limited in range from India to Australia, petering out with one species in Tasmania which is also found around Mt. Kosciusko in New South Wales. The subgenus *Parasarcophaga* is abundant in the Holarctic and Ethiopian regions, reaches Australia, and the one species in Tasmania is dominant over the southern half of the mainland. Each of these Tasmanian species has the aedeagus slightly out of harmony with those of the more tropically-situated allies, being not so highly developed. The typical subgenus *Sarcophaga* is limited to the small *carinata*-group in the Palaearctic region and the larger *crinata*-group which ranges from India to Queensland. Of the three subgenera, *Chrysosarcophaga* appears to preserve best the more primitive general characters and so supports the theory.

The Lower Brachycera show a similar feature, as for instance in the Stratiomyidae, the Pachygasterinae, a subfamily considered by James (1936) to be the most advanced one, has dominance in tropical regions and is reduced to four species in two genera within Tasmania; but structural details are not fully understood. On the other hand, the genus *Odontomyia* represents a much older type and is showing a far advanced trend towards elimination from tropical and subtropical areas. It is abundant in northern and southern temperate zones, and only one species is found in northern Australia, the majority, seven of the ten known Australian species, occurring in Tasmania.

A distribution still more reduced is seen with Apioceratidae. The genus *Apiocera* is known from southernmost Africa, the Australian mainland and Chile, whilst outside this Gondwana distribution, it is found only in the Rocky Mountain area north of Mexico to the Canadian border. The remaining three genera of the family are similarly distributed, one each occurring in three of these areas, Africa alone being excepted.

Ceratomerinae is a subfamily of Empididae restricted to Australia, New Zealand and Chile, whilst *Pelecorhynchus* is confined to the first and last of these.

Here, then, is seen a sequence of diminishing areas of dispersal, a dwindling in habitat that may be reflected throughout the Brachycera and that logically leads to endemic forms like *Exeretoneura* (Nemestrinidae) that become limited to south-eastern Australia and even to Tasmania only, and there are many other types of Brachycera that similarly support the theory of poleward dispersal. This general diminishing area of dispersal may also bear upon the relative age of the types discussed, but there is no evidence to show in which epochs they were respectively dominant.

Conclusion.—The general view that may be gathered from these remarks, suggests that in whatever way the isolation of *Pelecorhynchus* in two areas of the southern hemisphere was brought about, the antarctic theory is likely to prove unsatisfactory, and if adopted, it is difficult to see the line along which the investigation will proceed. The opposed theory has the advantage, at present, in that it not only avoids building a theory upon a theory, but also opens the way to a comprehensive search for data.

SUPERFAMILIES OF DIPTERA.

During the hundred years from Latreille (1825) to Tillyard (1926), several authors have arranged this order under groups higher than families, and of these Coquillett (1891) introduced the first simplified system based upon the modern conception of superfamilies.

The practical difficulty experienced hitherto in accepting superfamilies lies in the fact that no characters on the adult were found to define their limits adequately. Malloch (1917) returned to the method of classifying on larval and pupal characters, which system was initiated by Brauer (1864), but succeeded in making little alteration to Brauer's plan in that very inconvenient way of arranging superfamilies, and no author subsequently has made use of the scheme. The attempt made by Tillyard, with the aid of the late A. L. Tonnoir, certainly improved upon the general scheme, bringing adult characters to bear upon superfamilies, but there, too, the result is universally regarded as unsatisfactory. The fresh effort made here, is based upon terminal characters of the male, and thus introduces a new set of characters for building up a stable classification.

Coquillett proposed using eight superfamilies under Latreille's two suborders, and Malloch increased this to twelve in the Orthorrhapha alone, making fifteen in all if those of the Cyclorrhapha be added. Tillyard reduced the number to twelve, but in the present paper only nine are regarded as valid, or if future adaptations are to be made in the Nematocera and Hippoboscoidea, this number still may be high.

Sections.—At present I can see no characters of sufficient importance upon which to use the grade "suborder" and make it worthy of comparison with those of other orders. Latreille proposed two primary sections, the Proboscidea and Eproboscidea, the latter being limited to one family, Pupipara (now Hippoboscoidea), and Walker (1848) raised these to suborders. Following upon ideas expressed by Osten-Sacken, Williston accepted three suborders in accord with (a) Nematocera, (b) the rest of the Orthorrhapha, and (c) the Cyclorrhapha, the two last names being the suborders of Brauer's scheme. To these White (1914) added a fourth suborder, Pupipara. Tillyard reduced this number to two once more, adopting Macquart's two primary divisions, Nematocera and Brachycera, and he restricted the name Orthorrhapha in both scope and status, regarding it as being a division of the suborder Brachycera. In this, Tillyard relied upon the view that evidence showed that the original dichotomy, though not yet complete, was undoubtedly into Nematocera and Brachycera. Williston pointed out that the soundest primary division was that proposed by Brauer, in so far as it contrasted by characters of the larva and pupa, to which may be added here the male terminalia, too.

Subsections.—It is advisable, as a temporary measure, to join superfamilies together under subsections so as to incorporate the name Nematocera. Other subsections of equal importance have names applied by early authors who conceived them to be major units. When the superfamily status within the Nematocera becomes understood, these subsection names will no longer be needed and will disappear from the classification.

Nematocera, based on Latreille's Nemocera, is used by all authors and only Lameere (1906) proposed modifying its scope. Brachycera was used by Macquart to cover the remainder of the order, but Schiner (1864) and some later authors use it in a restricted sense. It stands as a comprehensive group unsuited for a subsection. Macquart proposed Entomocera to cover the major part of the Tabanoidea, and Aplocera to cover the remainder of the Brachycera. Although Tanystoma originally covered part of the Tabanoidea, Latreille finally restricted its scope under Notacantha, Tabanidea and Tanystoma where it became available for the Asiloidea. Macquart used the name in this sense, but Brauer and Malloch needlessly transferred the name to the Tabanoidea which had been eliminated from its scope.

Aschiza Brauer covers Syrphoidea as a subsection, remarked upon by Macquart but left unnamed by him, whilst his Dichaeta covers the same scope as does the later Schizophora Brauer. Macquart's divisions Calyptrata and Acalyptrata* arise from

* In his *Diptères Exotiques*, Macquart used Calyptrata and Acalyptra, the latter being an obvious error. I know not who amended this by omitting the "e", and there are other variations used, such as Calyptrae and Acalyptrae.

Calypteratae Desvoidy which, in the original sense, contained at least parts of the families Oestridae, Muscidae, Calliphoridae (including Sarcophaginae), Tachinidae and Conopidae, but excluded Phaoniinae, Anthomyiinae, etc. Macquart amended this faulty conception but excluded the Oestridae, an error subsequently rectified. The name Calyptrata now covers a slightly wider division than does the earlier Creophiles Latreille that has been allowed to lapse.

Myodaires was used by Desvoidy with no definite conception in the classificatory sense, but was convenient as a substitute for *Musca sensu lato*, when *Musca* had become very restricted. The modified name Myodaria, as far as I have traced, was first used by Lameere to balance Syrpharia (now Syrphoidea), whilst Williston used it to balance Pupipara, and in both cases it remains identical with Dichaeta.

Superfamilies.—On terminal structures of the male, the Brachycera fall into four divisions. Those of the Tabanoidea are like those of the Nematocera, the primitive claspers being hinged to swing horizontally towards each other. Claspers on the Asiloidea swing vertically, parallel with each other, or become fused at their bases with the apex pointing upwards. The terminal segments of the Syrphoidea take a semi-circular bend to the right, and when at rest, the aedeagus is protected in a phallic pouch formed in the pleural region about the sixth segment. There are no claspers here, but secondary claspers appear in the fourth division where the phallic pouch forms part of a large completely enclosed genital cavity. There are no intermediate forms known between these four divisions, each having its distinctive and clear-cut type of male terminalia.

Coquillett proposed seven superfamily names, of which six still stand: Tipuloidea, Bibionoidea, Tabanoidea, Asiloidea, Syrphoidea and Muscoidea. In the Nematocera, Malloch added four more, two surviving: Cecidomyioidea and Culicoidea. Tillyard remodelled this on the basis of six superfamilies, but only the four mentioned are retained.

Under the Brachycera Orthorrhapha, Malloch used six superfamilies, reduced to three by Tillyard, but only two by Coquillett are accepted here: Tabanoidea and Asiloidea. Throughout literature, under Cyclorrhapha, three superfamilies are accepted, proposed by Coquillett who, however, did not designate a name for the Hippoboscoidea. The resulting classification now stands as follows:

Order.	DIPTERA.
Section.	Orthorrhapha.
Subsection.	Nematocera.
Superfamily.	Tipuloidea.
	Culicoidea.
	Cecidomyioidea.
	Bibionoidea.
Subsection.	Entomocera.
Superfamily.	Tabanoidea.
Subsection.	Tanystoma.
Superfamily.	Asiloidea.
Section.	Cyclorrhapha.
Subsection.	Aschiza.
Superfamily.	Syrphoidea.
Subsection.	Dichaeta.
Superfamily.	Muscoidea.
Division.	Acalyptrata.
	Calypttrata.
Superfamily.	Hippoboscoidea.

Brachycera

In a criticism of my original draft on the classification of Diptera, Dr. C. P. Alexander states that: "In whatever superfamily the Psychodidae are placed, the Tanyderidae must be placed in the same", and he thinks there would be no objection in adding the Psychodidae to the Tipuloidea. Also I note that it may be necessary to amalgamate the Culicidae with the Tipuloidea in the event of a further reduction in the number of acceptable superfamilies, and judging from structures that I have been able to find in the Bibionoidea, this superfamily may include characters on the male terminalia that are more primitive than any I have seen in the Tipuloidea so far studied. Because of its approach to the Brachycera, there is a tendency to regard the Bibionoidea as advanced in respect to the Tipuloidea, whereas the true position may be found when the terminalia are intensively studied. Probably the Tipuloidea represent a side issue derived from a low position in the sequence of development towards the Brachycera, and the Bibionoidea lie nearer to the direct sequence.

In listing nine major trends in the evolution of flies, Williston pointed out that "all or nearly all . . . are polyphyletic, resulting in numerous cases of parallel resemblance which must be taken into account in any attempt at a true classification". This applies also to the terminal characters, but everywhere occasional characters are added and widely repeated over the order, and any failure in recognizing their status may bring divergent views on the evolutionary sequence at least. It becomes difficult, therefore, to assess the phylogenetic relationships between superfamilies, but the four under Nematocera are in accord with the divisions apparently seen by the late F. W. Edwards, and it is expedient that I should accept this and place it upon a superfamily basis awaiting further information. Some slight amendments may be needed in the Brachycera, but the main work seems to have been covered there.

Jobling (1936), writing on Streblidae, regards this family as belonging to the Acalypttrata, and the family Hippoboscidae is said to have its affinities with the Calypttrata, thus making the Hippoboscoidea a complex, but it is convenient to retain the superfamily until the affinities can be assured.

Key to Superfamilies of the Diptera.

1. Male terminalia of primitive rectilinear form, or else curvilinear with the eighth and ninth tergites adjacent to each other. Coxopodites are present ORTHORRHAPHA . . . 2
Male terminalia either curvilinear combined with an inverted hypopygium, so that the ninth tergite is adjacent to the eighth sternite, or else completely circumverted. The aedeagus is always directed anteriorly, lying within a phallic pouch formed normally within the fifth and sixth abdominal segments. Coxopodites always absent. . . CYCLORRHAPHA . . . 7
2. With claspers hinged to swing towards each other within 45 degrees of the horizontal plane, and attached to laterally placed supports (basistylus of taxonomists). Terminalia of varied forms, but never curvilinear and the aedeagus is always directed rearwards . . . 3
With claspers hinged to swing in the vertical plane, or fused with the apex directed upwards. Terminalia of varied forms, including the simple curvilinear type in which the aedeagus is often directed forwards, but never lies within a phallic pouch. ASILOIDEA
3. With pulvilliform empodium. Palpi never more than two-segmented and rarely do the antennae have more than three or four articulating segments TABANOIDEA
Without pulvilliform empodium. Palpi normally with four to six segments and the antennae usually with many articulating segments 4
4. With the median cell present, or if absent then two anal veins are complete. Failing this (Psychodidae) the body and wings are densely hairy, and normally the wings are held roof-like over the abdomen TIPULOIDEA
Without the median cell and never more than one anal vein is present. Never densely hairy on wings, but if dense scales occur, these are limited to the veins 5
5. Due to the folding of wings during pupal development, the adult may have a network of, or fan-shaped, creases. When these are not present, the wings are broad and at least have a distinct anal lobe and well-developed venation. If the radial field be reduced below four branches, then the median field has at least three branches. In Scatopsidae the veins may be very weak and overlooked, but the broad form of the antennae (typical Bibionid type) relegates the species to this superfamily BIBIONOIDEA
Wings never with such creases and the anal lobe is not developed, or if slightly so, then the venation is much reduced. Antennae always slender 6
6. Ocelli never present and usually the venation is fairly complete, the radial vein being four-branched, or if less than four branches occur in the median field. At the maximum reduction (Chironomidae which has less than 16 segments in the antennae) at least one vein occurs in the median field. Proboscis often formed for blood-sucking . . . CULICOIDEA

- Ocelli present (Mycetophilidae) or absent (Cecidomyiidae). In the latter case the veins of the median field are entirely absent. Subdivisions of antennal segments increase their number to about 30 normally, and may become excessive; never less than ten segments are present CECIDOMYIOIDEA
7. With the upper lamella retained as a pair of swollen tubercles lying one each side of the anus thus: (O), the "O" representing the papilla and the parentheses representing the divided lamella. The armature of the aedeagus is normally large and complex and no secondary claspers are developed. The primitive phallic pouch is usually placed latero-ventrally SYRPHOIDEA
- With lamella eliminated. Terminalia always circumverted with the genital cavity opening ventrally, the concealed genital pouch forming part of the cavity. Armature of the aedeagus very restricted or absent. One or two secondary claspers frequently developed 8
8. Normal flies with coxae nearly always placed close together. Abdominal sclerites nearly always clearly defined and separated, but occasionally some may fuse together. Parts of the male terminalia usually all present MUSCOIDEA
- Abnormal flies with coxae spaced widely apart and usually most or all abdominal segments are fused together. Parts of the male terminalia are vestigial or eliminated. Flies parasitic on vertebrates HIPPOBOSCOIDEA

Evolution of claspers.—As authors mostly assume all types of claspers to be homologues, an idea not now tenable, an explanation must be given for their treatment in the above key. Snodgrass, in his *Principles of Insect Morphology*, 1935, uses the terms *coxopodite* and *harpago* for parts that Tillyard calls the *lateral gonapophyses*, whilst the terms gonapophyses is restricted by Snodgrass to a structure that does not occur on Diptera. If the coxopodite and harpago truly represent a limb then, in the primitive form, both must have had a vestiture. In Simuliidae such a vestiture is found equal in density on each part and also the harpago may have some of the hairs thickened to bristles, their number varying with the species. Bristly hairs are found also on the harpago of Tipuloidea and Culicoidea where other vestiture is absent. Vestiture entirely disappears in higher families of Nematocera and is unknown to me in Tabanoidea and Bombyliidae. On other Asiloidea the remnant of vestiture occurs on *Apiocera* in the form of bristly hairs on the claspers, and here, as elsewhere (Bombyliidae excepted), a very significant change already has taken place within the superfamily, namely, lower forceps developed forming a partly enclosed genital cavity.

The lower forceps arise as an extension of coxopodites and bear the same vestiture. Attached to the inside is a pair of claspers which, apparently, are not homologous with the harpagones (primary claspers). Probably they are part of the forceps curved inwards, differentiated by a cleft along the line of curvature, remaining somewhat generalized with bristly hairs on some species of *Apiocera*, and becoming clasper-form both with and without bristly hairs on others; the harpagones quite disappear.

The coxopodites, harpagones and lower forceps do not form on Cyclorrhapha, where yet another change is traceable through the now well-known alteration that takes place with the sclerites. The apical or ninth segment (hypopygium) becomes inverted and, from the sixth onwards, the segments take a spiral formation that brings the ninth segment to the erect position once more, the circumversion of the hypopygium being thus completed. In addition, the whole of the modified segments concerned take a curve to the right, bringing the aedeagus into a phallic pouch situated in the pleura, as seen in Syrphoidea where no claspers occur, and instead, an armature developed at the base of the aedeagus and in continuity with it.

Under this new condition the sixth and ninth sternites and the seventh and eighth tergites are on the inner curve, and they become reduced or eliminated in conformity with the amount of development that has taken place. In Calyptrata, where the development is moderately advanced, the aedeagus has moved forwards, dividing the remnant of the ninth sternite, and again still further forwards, dividing the remnant of the eighth tergite, too. Thus arises a pair of remnants each side of the aedeagus in Muscoidea and these are called claspers.

Snodgrass refers to these as a pair of free lobes arising from the ninth sternite, thus indicating their position but not their origin, and moreover, he has assumed the sixth segment is eliminated in order to justify his method of numbering sclerites.

Other authors have disputed whether it be the sixth, seventh or eighth segment that is missing, but I find that, with my own interpretation, it is quite unnecessary to assume the loss of a segment, for which reason I think the present account of origins is likely to prove satisfactory.

Superfamily TABANOIDEA.

In this superfamily five main stems have been traced, and of these, the Stratiomyid-stem has developed not only a specialized venation, but also shows a very varied abdominal shape with the flattened or depressed type prevailing, reaching the disc form as in Pachygasterinae. The Cyrtid- and Nemestrinid-stems also have a specialized venation, the former again showing a variety of abdominal shapes. The Tabanid-stem has the abdomen depressed, reaching oval-depressed, but one form known to me is short cylindrical, and the South American genus *Acanthocera* has some species with clubbed abdomens.

The Tabanid-stem, with normal venation, arises from the Leptid-stem, which is regarded by universal consent as being the more primitive, and shows a tapering cylindrical abdomen together with the advanced sphero-conical form as on *Dasyomma*. When arranged in phyletic sequence showing the varied stages reached from cylindrical to sphero-conical shaped abdomen, it is noted that this change is mainly associated with an increase in capacity relative to surface area, and so the trend towards the depressed form might be associated with maintaining a more consistent relationship between capacity and area of surface, a phenomenon bearing, presumably, upon development in egg capacity and physiological changes connected therewith.

This is more readily seen in Asiloidea as the number of eggs estimated for Asilidae with cylindrical abdomens is 100 or less as against 300 and 400 for other more advanced shapes, but the present information is rather scanty. The capacity of blowflies with sphero-conical abdomens is found to be 2,000 eggs and of members of the genus *Oncodes* (Cyrtidae), which have very distended abdomens for their size, is many thousand minute eggs.

As no suitable key has yet been given to cover the Australian Tabanidae, the following one to subfamilies may prove of use. A few difficulties need to be overcome before a key to genera is formed.

Family TABANIDAE.

Key to Subfamilies of the Tabanidae.

1. Abdomen nearly sphero-conical or somewhat approximating to that form. There are four or five normal segments visible, the sixth and remainder being highly reduced, tubular and incorporated with the genital segments. Hind tibiae with spurs .. *Pelecorhynchinae*
Abdomen with seven normal segments visible 2
2. Hind tibiae with spurs *Pangoninae*
Hind tibiae without spurs *Tabaninae*

Recently Mackerras and Fuller (1942) proposed raising the *Pelecorhynchinae* to family status on larval characters, and they discuss the position regarding the adult characters. The authors, however, fall to the usual error of regarding as primitive some characters not yet proved to be so, and they make their remarks with this bias. There are now twelve or more family names proposed, arising from studies on Tabanoidea, seven being monotypical or nearly so, and the movement to add to their number has not yet ceased.

Subfamily PELECORHYNCHINAE.

Modern researches on terminalia do not bear out the statements that "The ovipositor of the female is, however, much more primitive than that of any Tabanid" and "the shovel-shaped eighth sternite with its cleft distal end, which, from its resemblance to the corresponding sternite of *Chorista*, . . . represent the most primitive condition found in Diptera" (Mackerras and Fuller, 1942, p. 28). Indeed, associated with these female terminalia, nothing is shown to be fundamentally primitive, but instead the data indicate a more highly advanced type than generally supposed. The reduced tenth tergite, the loss of the suranal plate (if it be not confused with the apparent two-segmented cerci), the lost ninth sternite (if perchance it be not combined with the

elongate eighth), enhance the idea of the ovipositor being an advanced type. Probably Mackerras and Fuller also err in their interpretation of that difficult feature, the male terminalia, in so far as they use the term "cerci", the presence of which is disputed on any male dipteran. In some cases the apparent cerci are remnants of the suranal plate, the eleventh tergite of some authors.

Genus PELECORHYNCHUS Macq.

Mackerras & Fuller, 1942, 45.—*Archeomyia* Philip, 1941, p. 3, genotype, *P. fulvus* Ric.

This synonym is not given by Mackerras and Fuller, who were unaware also that Philip suggests the genus *Bequaertomyia* Brennan, based on a rare and more primitive species on the Pacific Coast of the United States, also belongs to the Pelecorhynchinae. *Archeomyia* is erected on the one character only, namely, the frons on the male being as broad as long and two-thirds as broad on *P. mirabilis*, but as the eyes are approximate on *P. distinctus*, the proposed genus does not conform to the *fulvus*-group. The comparative width of the frons does not seem a reliable character for generic erection on any of the Australian Brachycera.

Subfamily TABANINAE.

Genus TABANUS.

Of the four sections into which this genus is divided, there are now 16 species, as shown below in the first, 37 in the second, and 2 in the fourth, leaving about 70 species for future consideration, nearly all of them belonging to the third section.

Section 1.

Tabanus posticus-group.

T. avidus-group, Hardy, PROC. LINN. SOC. N.S.W., lxiiv, 1939, 42.

Distinguished by the frons being 5 and 6 times longer than broad. So far this is the only group brought under the section, and the distribution of the species suggests that some of them may be subspecific in value or even less. Natural units may be observed by grouping in the list below, the first and second, the third to sixth, the seventh to ninth, the eleventh to thirteenth, and the fifteenth and sixteenth.

Key to Species of the T. posticus-group.

- | | |
|---|---|
| 1. Callus long, reaching well beyond the middle of frons | 2 |
| Callus reaching to about, or before, middle of frons | 6 |
| 2. Antennae yellowish-brown | 3 |
| Antennae black | 4 |
| 3. Upper section of callus linear | <i>torressi</i> |
| Upper section of callus tapering | <i>palmensis</i> |
| 4. Whitish hair-spots on median line of abdomen large and distinct | 5 |
| Whitish hair-spots on median line of abdomen small and weak or absent | <i>wentworthi</i> , <i>laticollosus</i> |
| 5. Upper section of callus linear | <i>magneticus</i> |
| Upper section of callus tapering | <i>doddi</i> , <i>alternatus</i> |
| 6. Antennae black or mainly so | <i>heroni</i> , <i>victoriensis</i> |
| Antennae lighter, red or at least yellow at base | 7 |
| 7. Appendix present in venation | 8 |
| Appendix absent | 9 |
| 8. Legs black and brown | <i>nigritarsis</i> |
| Legs yellowish | <i>ochraceoflavus</i> |
| 9. Dark species. Legs black or brown, only tibiae yellowish | <i>duplonotatus</i> , <i>davidsoni</i> |
| Yellow or yellow-brown species. Normally with yellow legs | 10 |
| 10. Small species up to 9 mm. Femora and tibiae may be dusky | <i>brevior</i> |
| Larger species above 12 mm. Legs always light coloured | <i>posticus</i> , <i>sanguinarius</i> |

T. torressi Ferg. & Hill 1922. ♀.—Islands of the Torres Strait.

T. palmensis Ferg. & Hill 1922. ♀.—Queensland; Palm Island.

T. doddi Taylor 1916 (*abstersus* Taylor 1913 in part, *nec* Walker), (*macquarti* Ricardo in part). ♀.—North Queensland.

T. alternatus Ferg. & Hill 1922 (*limbatinervis* Macquart 1849, preocc. Macq. 1847), (*macquarti* Ricardo 1915, preocc.), (*abstersus* Taylor in part). ♀.—South Queens-

- land and New South Wales. According to Taylor, South Australia as well, but this needs confirmation.
- T. alternatus* var. *magneticus* Ferg. & Hill 1922. ♀.—Queensland; Magnetic Island.
- T. wentworthi* Ferg. & Hill 1922. ♂, ♀.—New South Wales; Blue Mountains.
- T. laticallosus* Ricardo 1914, *nec* Taylor (*rufoabdominalis* Taylor 1917). ♂, ♀.—South Queensland; Moreton and Stradbroke Islands. New South Wales; Byron Bay.
- T. heroni* Ferguson 1921. ♀.—New South Wales; Dorriggo. Ferguson & Hill place this as a variety of *laticallosus* and hardly separable from *victoriensis*.
- T. victoriensis* Ricardo 1915. ♀.—New South Wales and Victoria.
- T. duplonotatus* Ricardo 1914 (*parviccallosus* Taylor 1917, *nec* Ricardo). ♀.—South Queensland.
- T. nigratarsis* Taylor 1913. ♀.—North Queensland and Northern Territory.
- T. davidsoni* Taylor 1919. ♀.—South Queensland and New South Wales. The record by Ferguson and Hill of a specimen from north Queensland needs confirmation.
- T. ochreoflavus* Ferguson & Henry 1919. ♀.—New South Wales; Camden Haven district.
- T. brevior* Walker 1848, *nec* Taylor 1919 (*marginatus* var. B Walker), (*anelosus* Summers 1912), (*australis* Taylor 1916), (*crypterythrus* Taylor 1919). ♂, ♀.—Northern Territory.
- T. posticus* Wiedemann 1828 (*Atylotus avidus* Bigot (1892), (*fuscipes* Taylor, 1913, *nec* Ricardo), (*taylori* Austen 1914). ♂, ♀.—Queensland and New South Wales. Ricardo suggested the identity of Wiedemann's species, but did not use the name. There can be little doubt that the synonymy is correct.
- T. sanguinarius* Bigot 1892 (*Atylotus*), (*nigropicta* Froggatt 1915, *nec* Macquart). ♀.—South Queensland, New South Wales and South Australia.

Superfamily ASILOIDEA.

A row of articulating spines is peculiar to this superfamily, each spine articulating in a membraneous ring on the apparent ninth tergite of the female. Centered around this structure have been many comments made usually on the idea that the character is recent in origin and isolated. Investigations show that it must have arisen early in the evolution of the Asiloidea as it becomes vestigial and disappears in the higher forms, but remains almost invariably present in the more primitive ones; *Phellus* is an exception.

This and other characters discussed in the prior notes (Hardy, 1942), when placed on a phylogenetic basis, brings the order of the families almost into alignment with that adopted by earlier authors and the subject may be summarized as follows:

Bombyliidae. There is but one plate, possibly the ninth and tenth tergites combined, bearing these articulating spines which are numerous and closely set together. They are consistent almost throughout the family.

Mydidae and *Apioceratidae*. The spines are fewer and more widely spaced, whilst along the median line of the tergite lies a ridge. This is on the apparent ninth tergite and no variations are known to me.

Asilidae. The ridge lying along the median line is detached in this family wherever found, and the spines are still present in the same form, but now lying on a pair of acanthophorites, one each side of the ridge. In the more advanced genera the ridge disappears, leaving the acanthophorites still divided, and these later become vestigial and disappear in advanced genera.

Therevidae. No ridge is present and the acanthophorites remain consistently paired and well formed; rarely if ever reduced beyond this.

Scenopinidae. Apparently the character has been lost throughout this family.

Empididae and *Dolichopodidae* are normally without the structure, but it becomes highly modified in the more primitive forms of the latter at least.

This order follows closely that proposed by Brauer in 1883, the difference being that the Bombyliidae are placed by him between Asilidae and Therevidae, so I believe the arrangement will be found satisfactory. Coquillett proposed making Apioceratidae, Mydidae and Bombyliidae, in this reversed sequence, into a separate superfamily, and the sequence of the first three names listed by him under Asiloidea is similarly reversed.

The primitive Asiloidean female terminalia given here (Fig. 1) is a composite figure showing a set of parts as would be seen from the latero-ventral aspect, with the pleural membrane of the eighth segment torn away to exhibit the gonopore lying within the genital groove bordered by a sclerite that represents, presumably, the ninth sternite which normally is hidden within the genital cavity. Many Asilidae have only the cerci missing, and they vary towards having most parts missing in the advanced forms, whilst

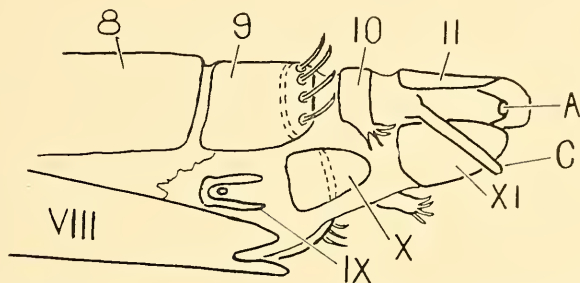


Fig. 1.—A composite figure of sclerites found on female terminalia of primitive genera of Asiloidea.

8, 9, 10, 11, the eighth to eleventh tergites respectively. A, the anal papilla. C, the cercus. viii, ix, x, xi, the eighth to eleventh sternites respectively.

The *acanthophorites* are represented by sclerite 9 which becomes divided along the median dorsal line. The *supplementary spines* occur on 10. The *suranal plate* if divided becomes the *dorsal lamellae* and is 11. The *ventral lamella* is xi. The *median plate* is x. The *chitin bordering the genital groove* is ix. The *genital cavity* is formed by x, ix, the apical part of viii, together with the membrane joining them. The *dorsal ridge*, not shown in the figure, is limited in length to the median line of the apparent ninth tergite, and may be in continuity with the *acanthophorites* or separated from them. When the upper lamellae are formed, they may be mistaken for cerci, if true cerci be absent. Cerci, however, are always distinctly separated from each other and the lamellae always adjacent to each other, as far as yet found. Invariably the so-called cerci on the males are the upper lamellae throughout the Asiloidea.

in the process of reduction, sclerites may become divided, or their shapes altered, or only minute remnants are retained. There are, however, gaps between some families, noticed in the sequence so far traced, and morphologically the structures are not certainly understood.

In the modern method of counting, the eighth tergite is normal, the ninth apparently has a row of articulating spines at the apex, but as this might be a complex of the ninth and part of the tenth segments, this sclerite is divided by a double dotted line. The apparent tenth tergite bears the supplementary spines arising from a flange forming an extension to this sclerite. The upper lamella forms the eleventh tergite covering the anal papilla from above, and in the primitive form it is a single sclerite (suranal plate); usually it is divided longitudinally and may disappear on *Dolichopodidae* where the cerci are retained in the form shown on the figure, namely, long and cylindrical. The ventral lamella becomes the eleventh sternite by this count, and may become weakened and disappear. The tenth sternite, in the primitive form, seems to be divided transversely as on *Apocerotidae*, but two trends are noted arising from this, one in which each half plate is divided longitudinally making four parts in all, as on *Bathypogon* and *Stenopogon*, the other in which the posterior half disappears and only an anterior pair of pieces remains; all, however, may disappear. The genital groove in which the gonopore lies, may have one, two or three ridges of chitin bordering it, but in the primitive form the ridge is found in one piece and U-shaped, forming the ninth sternite. The eighth sternite is normal with the usual cleft at its apex.

This interpretation is based upon the view that the abdomen is eleven-segmented, and if the figure be interpreted on a ten-segment or a twelve-segment basis, then it would be necessary to presume new structures arose in the former case, and in the latter the cerci are either misplaced or are needing some other origin to explain them. Mackerras and Fuller (1942) have given drawings for some terminalia of female *Tabanoidea* and

these are in alignment with the present interpretation. Other authors available to me find, apparently, only nine segments and the proctiger which is left unnumbered. Snodgrass (1935) uses only the Cyclorrhapha and Tipulidae in his interpretation, but his Panorpid figure agrees with the present numbering, his eleventh segment being the proctiger with two-segmented cerci. It is not certain if this method of numbering be correct.

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I have to thank Dr. C. P. Alexander for criticisms of my first draft on classifications of Diptera compiled from all authors available, and of which the above summary forms an amended abridgement; and also Colonel Cornelius B. Philip for drawing my attention to a paper which discusses the Pelecorhynchinae and which was not included in the studies by Mackerras and Fuller. I would also draw attention to Dr. G. C. Crampton's discussion on Phylogeny in the *Guide to the Insects of Connecticut*, Part iv (Diptera), 1942, pp. 115-8, where tentative suggestions are made concerning lines of descent. Here the conception of superfamilies is quite at variance with mine, making three superfamilies out of my conception of Tabanoidea, and three more under Asiloidea, one being Bombyloidea, including Nemestrinidae, Bombyliidae and Cyrtidae. This paper follows current ideas, bringing together some admittedly doubtful relationships, and was not taken into account in the above discussion, being too recent and apparently subject to wide alterations in the near future.

References.

- BRAUER, F., 1883.—*Denkschr. Akad. Wiss. Wien*, 47: 11.
 COQUILLETT, D. W., 1891.—*Proc. U.S. Nat. Mus.*, 33: 653-8. (*Smithsonian Inst. Publ.* No. 1227.)
 EDWARDS, F. W., 1923.—*Trans. N.Z. Inst.*, 54: 265-7.
 HARDY, G. H., 1942.—*Proc. Linn. Soc. N.S.W.*, 67: 197-204.
 ———, 1943.—*Ibid.*, 68: 17-23.
 JAMES, M. T., 1936.—*Ann. Ent. Soc. Amer.*, 29: 642-6.
 JOBLING, B., 1936.—*Parasitology*, 28: 355-366.
 LAMEERE, A., 1906.—*Mém. Soc. ent. Belg.*, 12: 105 (not seen).
 LATREILLE, M., 1834.—In Cuvier's *Animal Kingdom*. 4: 312-381. (A translation from the original French edition of 1825, and published by Henderson, London.)
 MACKERRAS, I. M., and FULLER, MARY E., 1942.—*Proc. Linn. Soc. N.S.W.*, 67: 9-76.
 MACQUART, J., 1838-55.—*Diptères Exotiques*, 2 volumes and 5 supplements.
 MALLOCH, J. R., 1917.—*Bull. Illinois Lab. Nat. Hist.*, 12: 161-407.
 PHILIP, C. B., 1941.—*Canad. Ent.*, 73: 2-14.
 SCHINER, J. R., 1864.—*Verh. zool.-bot. Ges. Wien*, 14: 193-212. (Not seen.) (Abstract in *Zool. Rec.*, 1864, p. 533.)
 TILLYARD, R. J., 1926.—*The Insects of Australia and New Zealand*. Angus & Robertson Ltd., Sydney, pp. 344-6.
 WALKER, F., 1848-55.—*List of Diptera in the British Museum*, 4 parts and 3 supplements.
 WHITE, A., 1915.—*Proc. Roy. Soc. Tasm.*, 1914, p. 36.
 WILLISTON, S. W., 1908.—*Manual of North American Diptera*, 3rd Ed., pp. 51-62.